

ON THE NATURE OF AGROBIONT SPIDERS

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ABSTRACT. Results from a 10 year survey of spiders in Hungarian arable and natural grassland habitats are cumulated in order to reveal the key characteristics of agrobiont species. We define agrobionts as species that reach high dominance in agroecosystems. The most dominant species, *Pardosa agrestis*, on average accounted for 40% of the total spider population in Hungarian arable fields. The presence of agrobionts led to a strong skew in arable spider community species distribution. Regardless of the over-dominance by agrobionts, arable spider communities had a potential for very high species richness. The agrobiont segment of arable spider communities showed very little field-to-field or regional variation, i.e. the same agrobiont species occurred in all fields. Agrobionts were indicators of arable habitats, and were rare in other habitat types, but in many species preferences for specific natural habitat types could be shown. These natural habitat types were often strongly abiotically driven, frequently disturbed habitats. The life cycle of agrobionts showed synchronization with the arable crop-growing season. While many closely related non-agrobiont species had maturity and reproductive periods either earlier or later than the main crop vegetation period, agrobionts invariably reached adulthood and reproduced during that period. Association with frequently disturbed natural habitats and phenological synchronization with the annual arable disturbance regime are such traits that support the theory that agrobiont species are adapted to predictably ephemeral habitats.

Keywords: Community structure, arable fields, cyclic colonization, life history strategy

Agricultural habitats are artificially created and maintained by periodic disturbances to be more uniform than most natural habitats. Agricultural systems have been present for only a short evolutionary time period. Thus they are likely to lack co-evolved animal communities. Many 'empty niches' may offer themselves for colonization both by herbivorous and predatory animals from natural habitats. It is still debated as to what degree these habitats are recolonized repeatedly, or to what extent they are self-perpetuating systems, at least at the metapopulation level (Duffey 1978; Bishop & Riechert 1990; Wissinger 1997). To study the community assembly rules in agricultural areas, and to study the ecological characteristics of the individual species should be revealing for the basic ecological phenomena, and may provide opportunities to shift the balance in agricultural communities towards beneficial organisms, and thus promote biological control.

Considering communities of predatory arthropods in agricultural areas, and those of spiders in particular, it has been observed that

a few super-abundant species often dominate these systems. The dominating species, since the seminal paper by Luczak (1979) are called 'agrobiont' species. The dominance of agrobionts has been established in various crops and geographical areas (Richman et al. 1990; Nyffeler & Breene 1992; Blick et al. 2000) but many questions about the ecological strategies of agrobionts are still open. Duffey (1978) and Luczak (1979) predicted that agrobionts are habitat generalists, "eurytopic" species, that occur sometimes in quite contrasting habitats. Recently Wissinger (1997) proposed that agrobionts are species with an "adaptation to predictably ephemeral habitats" (APEH). According to the APEH hypothesis agrobionts are not generalist species, rather they evolved a specific strategy, called the "cyclic colonization" strategy. Through cyclic colonization, agrobionts can escape the regularly occurring disturbances by dispersing to permanent refugia. The strategy requires specific life history adaptations, with special regard to synchronization with the periodic disturbances through the timing of reproduc-

Table 1.—Sampling locations that provided data for the meta-analysis. (A = alfalfa, C = cereal, G = grassland (No. of sub-types), P = pitfall, D = suction sampling.)

County	Settlement	No. of sites	Habitats	Method
Baranya	Nagyharsány	1	G(2)	P
Csongrád	Királyhegyes	2	A, G(2)	P, D
Heves	Hatvan	1	C	P
Heves	Recsk	1	G(1)	D
Nógrád	Bánk	1	C	D
Nógrád	Diósjenő	1	A	D
Nógrád	Pásztó	1	C	D
Nógrád	Rétság	1	C, G(1)	D
Nógrád	Romhány	1	A, G(1)	D
Pest	Kartal	2	C	P
Pest	Nagykovácsi	3	A, C, G(2)	P, D
Pest	Páty	3	A, C, G(1)	D
Pest	Budapest	1	G(1)	P, D
Tolna	Decs	1	A, C	D
Tolna	Felsőnána	5	A, C	P, D
Tolna	Szekszárd	1	A, C	D
Tolna	Tevel	1	A, C	P, D
Vas	Szombathely	2	C	P
Veszprém	Somlóvásárhely	1	G(1)	P

tion, and the presence of various colonizer and overwintering stages. Other ecological characteristics, such as competitive ability (Marshall & Rypstra 1999), tendency for cannibalism and intraguild predation (Wagner & Wise 1996; Hodge 1999; Samu et al. 1999b), and colonization power (Richter 1970; Sunderland & Topping 1993; Marshall et al. 2000) are additional features that might be important characteristics of the agrobionts' ecological persona. Although the importance of life history characteristics has been stressed in earlier studies (Duffey 1978; Toft 1989), no comprehensive comparisons of regional agricultural spider faunas and those occurring in natural habitats has been made, to date.

The present paper tries to reveal the ecological nature of the agrobiont species in Hungarian arable fields. We hope to find common ecological features of agrobiont species, and in this way get closer to their secret of being successful in human influenced habitats. Agrobionts are characterized through a meta-analysis of 10 years of survey data on spider assemblages of Hungarian arable fields. In the meta-analysis we seek to clarify (i) which are the main agrobionts in Hungarian arable fields; (ii) how the presence of these superdominant species affects the diversity and

dominance structure of the whole spider community, as compared to natural grassland communities; (iii) how agrobiont compositions vary field-by-field and regionally; (iv) what the original natural habitats of the agrobionts are; and (v) what commonalties can be found in their life cycles, and how do these relate to the disturbance regime of arable fields?

METHODS

Arachnological results from various faunistic and agro-ecological projects on arable fields (Samu et al. 1996; Tóth & Kiss 1999; Szinetár & Miltényi 2000; Samu et al. 2001) were accumulated into a common database (Samu 2000). The present paper provides a meta-analysis of these data, focused on the ecology of agrobiont species.

The sampling methods were pitfall trapping and hand-held suction sampling. Original survey datasets contained information on c. 110,000 individuals, but we restricted the scope of the analysis by the following criteria: (i) only adults were considered; (ii) only those data sets were included in which sampling lasted for at least one year for the given field/habitat patch and for the given method, and (iii) the total catch of spiders was greater than

Table 2.—The 16 most dominant arable (cereal and alfalfa) spider species. Last two columns indicate the percentage of fields a species was present out of all the fields sampled by the respective method.

Species	Family	Total catch	Dominance (%)	In suction sampled fields (%)	In pitfall sampled fields (%)
<i>Pardosa agrestis</i> (Westring 1861)	Lycosidae	10,423	38.96	88.46	100.00
<i>Meioneta rurestris</i> (C. L. Koch 1836)	Linyphiidae	3,886	14.53	100.00	58.82
<i>Oedothorax apicatus</i> (Blackwall 1850)	Linyphiidae	3,602	13.46	65.38	82.35
<i>Pachygnatha degeeri</i> Sundevall 1830	Tetragnathidae	1,683	6.29	80.77	94.12
<i>Erigone dentipalpis</i> (Wider 1834)	Linyphiidae	1,239	4.63	80.77	47.06
<i>Tibellus oblongus</i> (Walckenaer 1802)	Philodromidae	546	2.04	92.31	35.29
<i>Drassyllus pusillus</i> (C. L. Koch 1833)	Gnaphosidae	346	1.29	15.38	88.24
<i>Xysticus kochi</i> Thorell 1872	Thomisidae	322	1.20	46.15	76.47
<i>Pisaura mirabilis</i> (Clerck 1757)	Pisauridae	279	1.04	65.38	23.53
<i>Robertus arundineti</i> (O.P.-Cambridge 1871)	Theridiidae	268	1.00	26.92	58.82
<i>Araeoncus humilis</i> (Blackwall 1841)	Linyphiidae	226	0.84	73.08	47.06
<i>Trichoncoides piscator</i> (Simon 1884)	Linyphiidae	216	0.81	15.38	29.41
<i>Mangora acalypha</i> (Walckenaer 1802)	Araneidae	202	0.76	61.54	11.76
<i>Zelotes mundus</i> (Kulczynski 1897)	Gnaphosidae	172	0.64	0	29.41
<i>Meioneta simplicitaris</i> (Simon 1884)	Linyphiidae	166	0.62	73.08	29.41
<i>Lepthyphantes tenuis</i> (Blackwall 1852)	Linyphiidae	148	0.55	38.46	41.18
other species	207 species	3,028	11.32		
Total		26,752			

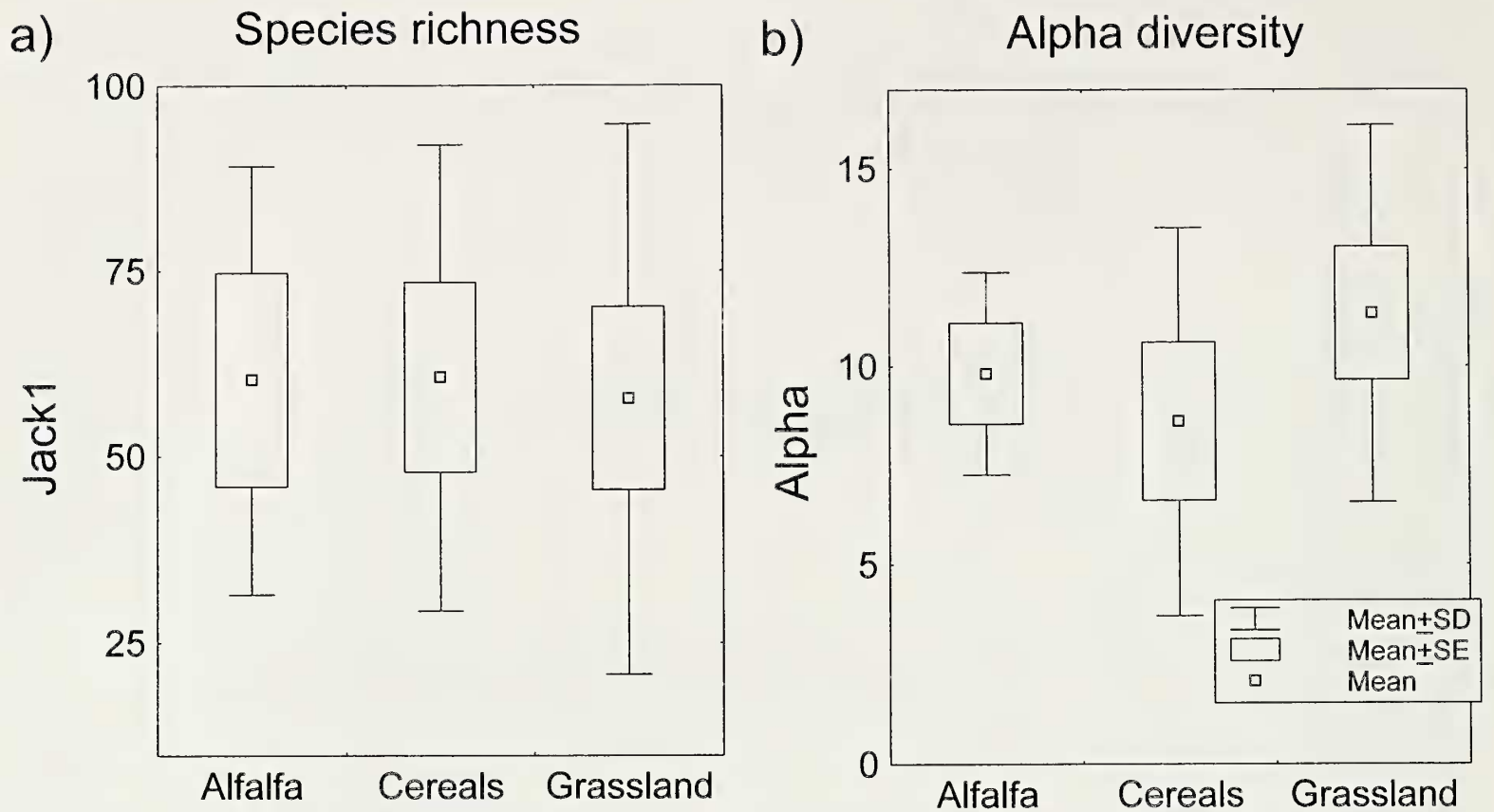


Figure 1.—a. Species richness (estimated by first order Jackknife estimator) and b. alpha diversity of spider communities of habitat patches/fields belonging to the main habitat types investigated.

100 adult individuals for the field; (iv) results were included from samples taken between 1990 and 2000. Since species composition is dependent on trapping method, and pitfall trapping yielded many more adults, community structure and field-by-field comparisons were made relying on pitfall trap data only.

The spatial unit of the analysis was a field

(fields were typically 30 ha, ranging between 1.5 & 250 ha), or the natural equivalent, a “habitat patch”. Samples conforming to the above criteria were taken in 47 field/habitat patches at 30 sites. The sites were in 19 localities in eight counties in Hungary (Table 1). The main sampled habitat types were cereal fields, alfalfa fields and natural or semi-natural grassland areas. Grasslands could be classified into five different sub-types: secondary, mesophile, saline, rock grasslands, and moist meadows. Secondary grasslands developed mainly on sites previously occupied by agricultural fields or intensive pastures, later abandoned but might receive occasional disturbances. They are colonized by numerous pioneering, introduced or ruderal species, but a natural regeneration has already started. The disturbance-induced simplified stratification is typical for the structure. Mesophile grasslands are a category for dense perennial grasslands of lowlands and hills, fertilized and well-drained. They are species rich grasslands with a complex structure. Light disturbance, such as occasional grazing or using them as hay meadows is possible. Saline grasslands are comprised of salt steppes and saltmarsh meadows (and all the continuum between them) of the Pannonic plain. Large expanses of salt steppe form an open landscape of short-grass

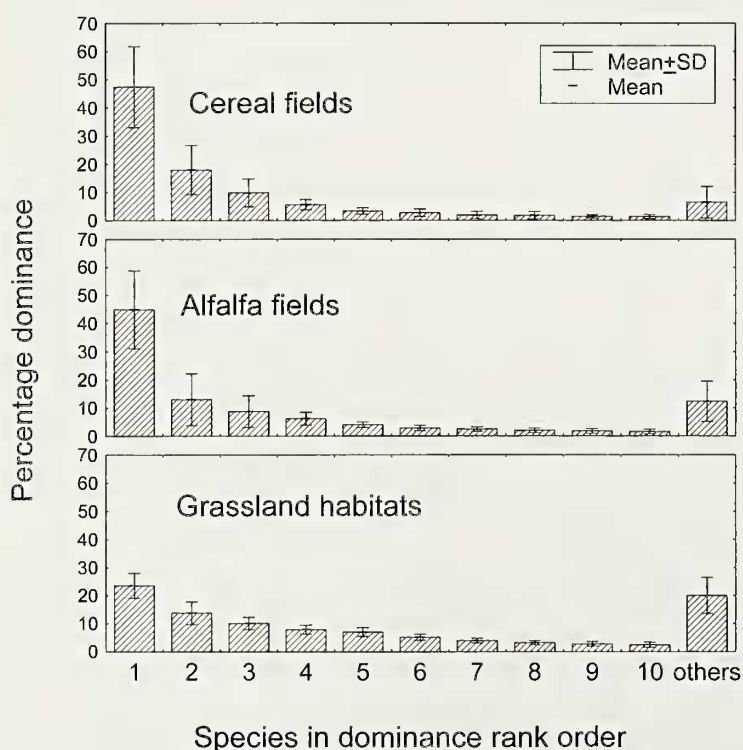


Figure 2.—The dominance structure of spider communities of habitat patches/fields belonging to the main habitat types investigated.

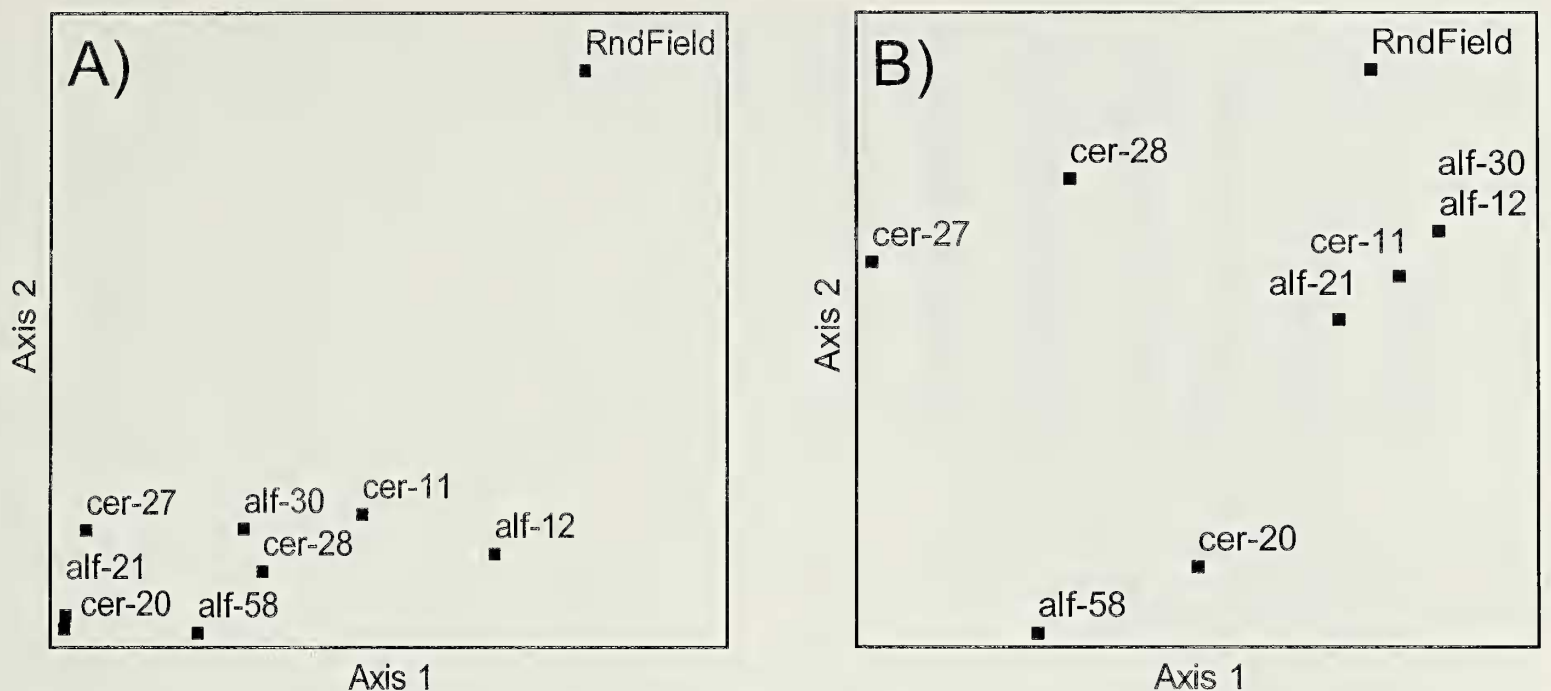


Figure 3.—Non-Metric Scaling (NMS) ordination plots, representing the Soerensen similarity structure of selected arable fields, when A) the first eight dominant species; and B) the second eight dominant species are considered. The random field was generated by shuffling mean dominances of the first 16 dominant species. (alf-x denotes alfalfa field; cer-x stands for cereal field, where x is identifier number of the given field; RndField denotes the hypothetical field where spider community was created by randomization [see text for details].)

swards on slightly elevated ground and of rills, eroded shallow depressions with bare or sparsely vegetated saline soils. Because of poor drainage, the rills experience yearly flooding in springtime, but dry out completely by summer. The structure is simple and open. Rock grasslands are xero-thermophile grasslands, on rocky areas or on rendzinas on hilly or montaneous areas. They occupy sites with a warmer, drier microclimate, in particular south-facing slopes with extreme conditions of insolation, temperature variation and evaporation. They are rich in plant species, but the structure is dominated by low grasses. Moist meadows develop on moderately to very nutrient-rich, alluvial or fertilized, wet or damp soils, often inundated at least in winter, and relatively lightly mowed or grazed. They include a large number of distinctive and often species-rich communities, many of which harbor specialized and rare species of plants.

RESULTS AND DISCUSSION

Agrobionts and agricultural spider communities.—Taken together all arable (cereal and alfalfa) data sets, a very distinctive list of the most dominant species arises (Table 2). The most dominant species are, by our definition, the agrobiont species. We regard any delimitation where a borderline between dom-

inant and non-dominant species should lie to be arbitrary, but considering a rather conservative 1% minimum dominance limit (i.e. an agrobiont species should be represented by more than 1% of all the individuals in the sampled assemblage) seems to be practical. It is also important to consider how widespread is the occurrence of a species in the considered crop(s). The rest of the analysis concentrates on the species listed in Table 2 and refers to species that occur on more than 75% of the fields and are above the 1% dominance threshold as “agrobionts”. Species that are below this limit, but still common in fields are called “agrophile” species after Luczak (1979).

Given the overwhelming dominance of agrobionts in arable fields, it is of interest to see how overall community structure is affected by them, what room is left for other species, and how agricultural spider community structure compares to the closest natural systems, grassland habitats. Species richness of cereal, alfalfa and grassland field/habitat patches was estimated from pitfall trap data with the first-order Jackknife richness estimator (Fig. 1a) using EstimateS (Colwell 1999), which gives a rather conservative estimate of species richness. Alpha diversity (Magurran 1988) for the same data set was

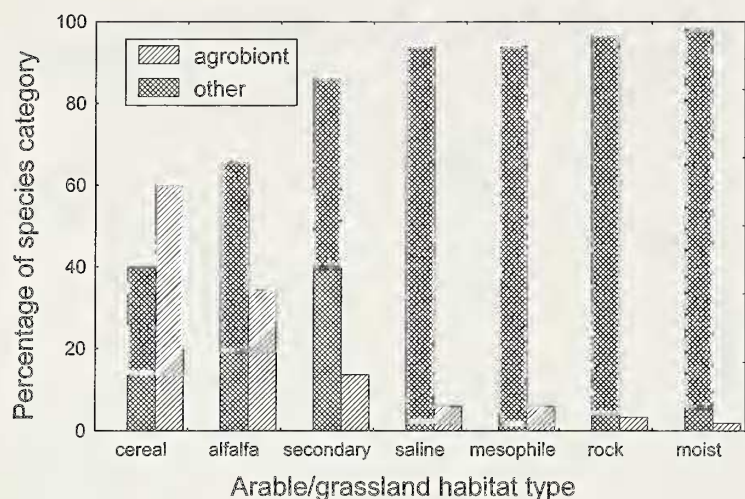


Figure 4.—Percentage representation of agrobiont spiders (first eight species in Table 2) in various habitat types in Hungary.

also calculated (Fig. 1b). Variation for both species richness and diversity values was high (mean $CV_{richness} = 54.0\%$, mean $CV_{diversity} = 43.3\%$, where $CV =$ coefficient of variation), and no significant difference could be shown among the different habitat types in either measure (one way ANOVA, richness: $F = 0.015$, $df = 2, 15$, ns; diversity: $F = 0.649$, $df = 2, 15$, ns).

While agricultural spider communities were not different in terms of species richness and diversity from the natural grassland communities, the dominance structure of the agricultural and natural communities showed a marked difference (Fig. 2). The first most dominant species of each field/habitat patch had a significantly higher dominance value in the arable habitats than in the grassland habitats (one way ANOVA: $F = 10.031$, $df = 2, 19$, $P < 0.005$, Tukey HSD test at $P = 0.05$: cereal and alfalfa ns, grassland significantly different from both). The descent of the dominance curves also differed significantly between arable and grassland habitats, being less steeply descending in the later (ANCOVA on log transformed dominance, habitat type*rank interaction: $F = 12.477$, $df = 2, 214$, $P < 0.0001$).

The high species richness and diversity found in some of the studied agricultural fields contradicts the traditional view of the impoverishment of these habitats (Nyffeler et al. 1994). While arable fields clearly have the capacity for high diversity, maybe it is even more important to point out large between field variability. Toft (1989) reported that two cereal fields were as diverse in Denmark as the best natural habitats; in Poland only about

Table 3.—Indicator species analysis (resulting in the species and habitat specific Indicator Value), conducted according to the method by Dufrene and Legendre (1997). P values were obtained by Monte Carlo analysis, performed by PC-ORD (McCune & Mefford 1999).

Comparison	Indicated habitat (where Indicator Value is maximal)	No. of indicator species ($P < 0.05$)	No. of agrobionts in indicator species	First three species, which significantly indicate the habitat
				cereal-alfalfa
cereal-grasslands	alfalfa	2	0	<i>Pardosa agrestis</i> , <i>Pachygnatha degeeri</i> , <i>Oedothorax apicatus</i>
	cereal	27	9	<i>Hogna radiata</i> , <i>Centromerus sylvaticus</i>
alfalfa-grasslands	grasslands	2	0	<i>Pardosa agrestis</i> , <i>Oedothorax apicatus</i> , <i>Pachygnatha degeeri</i>
	alfalfa	15	7	<i>Ozyptila atomaria</i>
arable-grasslands	grasslands	1	0	<i>Pardosa agrestis</i> , <i>Pachygnatha degeeri</i> , <i>Oedothorax apicatus</i>
	arable	26	8	<i>Centromerus sylvaticus</i> , <i>Hogna radiata</i> , <i>Ozyptila pullata</i>
grasslands	grasslands	7	0	

Table 4.—Habitat preferences of some agrobiont and agrophile spider species. Data obtained from Hänggi et al. (1995). (Abundance values were summed after giving values to abundance categories as follows: Rare = 1, Fairly common = 5, Common = 10 individuals.)

<i>Pardosa agrestis</i>			<i>Meioneta rurestris</i>			<i>Oedothorax apicatus</i>		
Habitat	Abund.	Habitat	Abund.	Habitat	Abund.	Habitat	Abund.	Habitat
Cereals	284	Cereals	264	Cereals	264	Cereals	612	
Cultivated grassland	224	Soil after surface mining	224	Soil after surface mining	205	Saline grassland	326	
Beet	100	Shrubs, hedges, cemeteries	100	Shrubs, hedges, cemeteries	165	Cultivated grassland	196	
Rye-grass/fertilized pastures	67	Brometalia	67	Brometalia	132	Beet	160	
Saline inland areas	60	Rye-grass/fertilized pastures	60	Rye-grass/fertilized pastures	107	Coastal dunes	117	
Pioneer areas	52	Potatoes	52	Potatoes	83	Rye-grass/fertilized pastures	116	
<i>Erigone dentipalpis</i>			<i>Pachygnatha degeeri</i>			<i>Drassyllus pusillus</i>		
Habitat	Abund.	Habitat	Abund.	Habitat	Abund.	Habitat	Abund.	Habitat
Saline grassland	366	Cereals	366	Cereals	467	Brometalia	71	
Cereals	310	Rye-grass/fertilized pastures	310	Rye-grass/fertilized pastures	318	Dry, semi-dry grasslands	61	
Cultivated grassland	270	Moist meadows	270	Moist meadows	241	Fers meadows	37	
Rye-grass/fertilized pastures	213	Cultivated grassland	213	Cultivated grassland	177	Hedges	32	
Lawns in parks	176	Fers meadows	176	Fers meadows	176	Forests edges	32	
Beet	160	Littoral areas, moist	160	Littoral areas, moist	145	Cultivated grassland	32	
<i>Xysticus kochi</i>			<i>Robertus arundineti</i>			<i>Araeoncus humilis</i>		
Habitat	Abund.	Habitat	Abund.	Habitat	Abund.	Habitat	Abund.	Habitat
Coastal dunes	202	Saline grassland	202	Saline grassland	127	Cereals	120	
Brometalia	95	Raised bogs	95	Raised bogs	37	Cultivated grassland	79	
Soil after surface mining	76	Dwarf shrub heath	76	Dwarf shrub heath	36	Clover, alfalfa	40	
Dry, semi-dry grasslands	59	Beet	59	Beet	31	Rye-grass/fertilized pastures	32	
Cereals	58	Moist meadows	58	Moist meadows	16	Saline inland areas	30	
Cultivated grassland	46	Cereals	46	Cereals	16	Brometalia	26	

Lycosidae life cycles

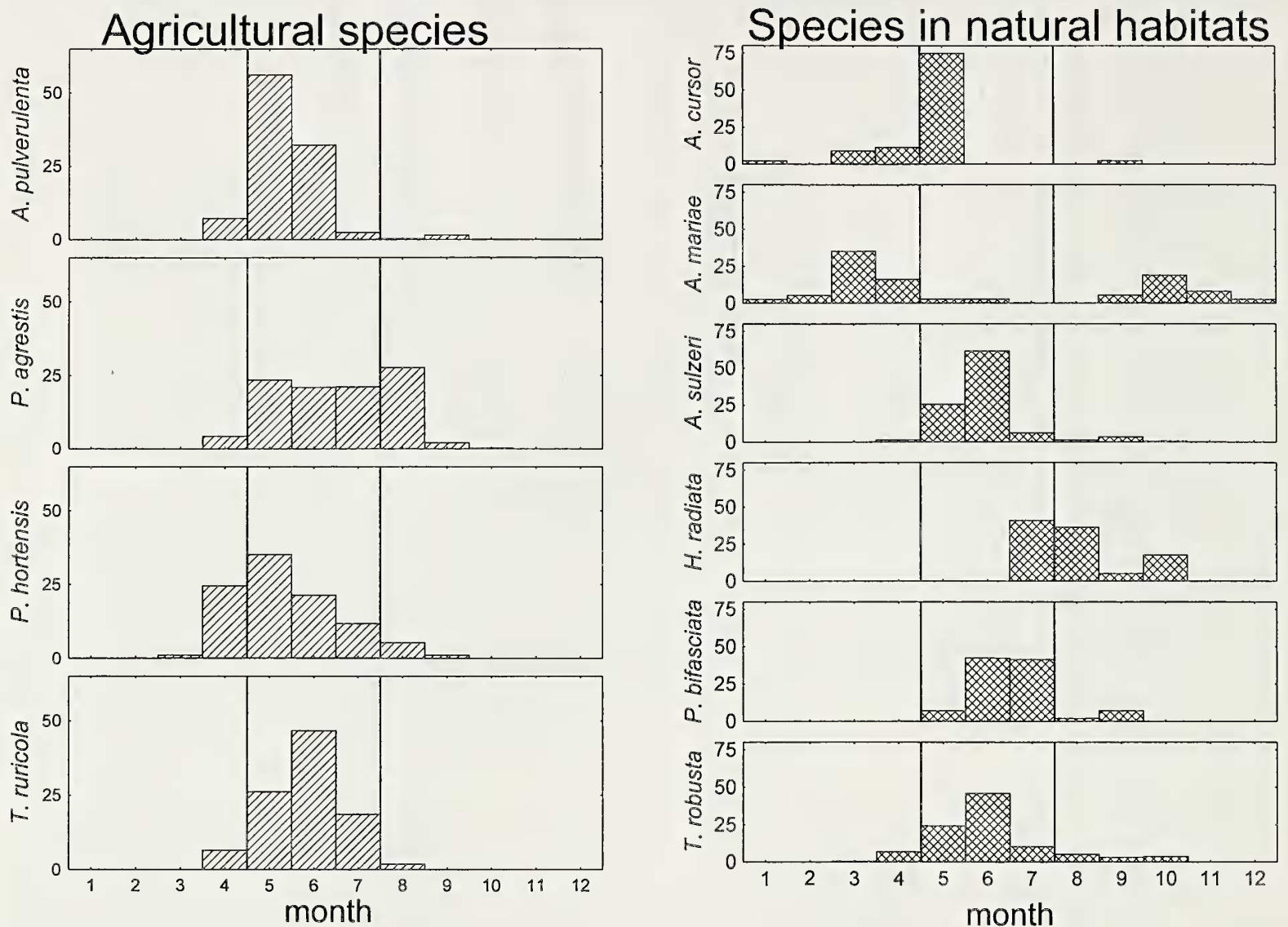


Figure 5.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Lycosidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Alopecosa pulverulenta*, *A. cursor*, *A. mariaae*, *A. sulzeri*, *Pardosa hortensis*, *P. bifasciata*, *Hogna radiata*, *Trochosa robusta*, *T. ruricola*.

half of that richness was found (Luczak 1975). Both in the US (Richman et al. 1990) and Hungarian (Samu et al. 1996) alfalfa fields there were also high between field and regional differences in spider species richness. The establishment of the causes for this variation is an important task for both agricultural ecologists and conservationists. There is likely to be multiple causation, including structural diversity (Sunderland & Samu 2000), management intensity, pesticide use (Altieri 1994; Jenser et al. 1999), field size, and landscape structure (Nyffeler & Breene 1992; Samu et al. 1999a; Tóth & Kiss 1999).

Variation in agrobiont composition of arable fields.—Unlike species richness, very little variation was found in the agrobiont composition of the different arable fields sampled. The first 8 species were virtually ubiquitous, and dominance orders showed very similar

patterns. To study the magnitude of similarity, 8 fields with large enough sample sizes were selected (4 cereal, 4 alfalfa), and, relying on pitfall trap data, the spider community of the first 16 most dominant species was considered (Table 2). A 'random field' was also generated, in which the average dominance values of the first 16 species were shuffled. The fields were ordinated by non-metric scaling (NMS) (Clarke 1993), first by the first eight most dominant species, then by species of dominance rank 9–16. The ordination plots show (Fig. 3), that regarding the first 8 dominant species, fields were similar to each other (mean Soerensen similarity \pm SD = 0.61 ± 0.145), and dissimilar to the random field, while for species of dominance rank 9–16 similarity to each other was much lower (mean Soerensen similarity \pm SD = 0.35 ± 0.140), and they were not as distinctly sepa-

Linyphiidae life cycles

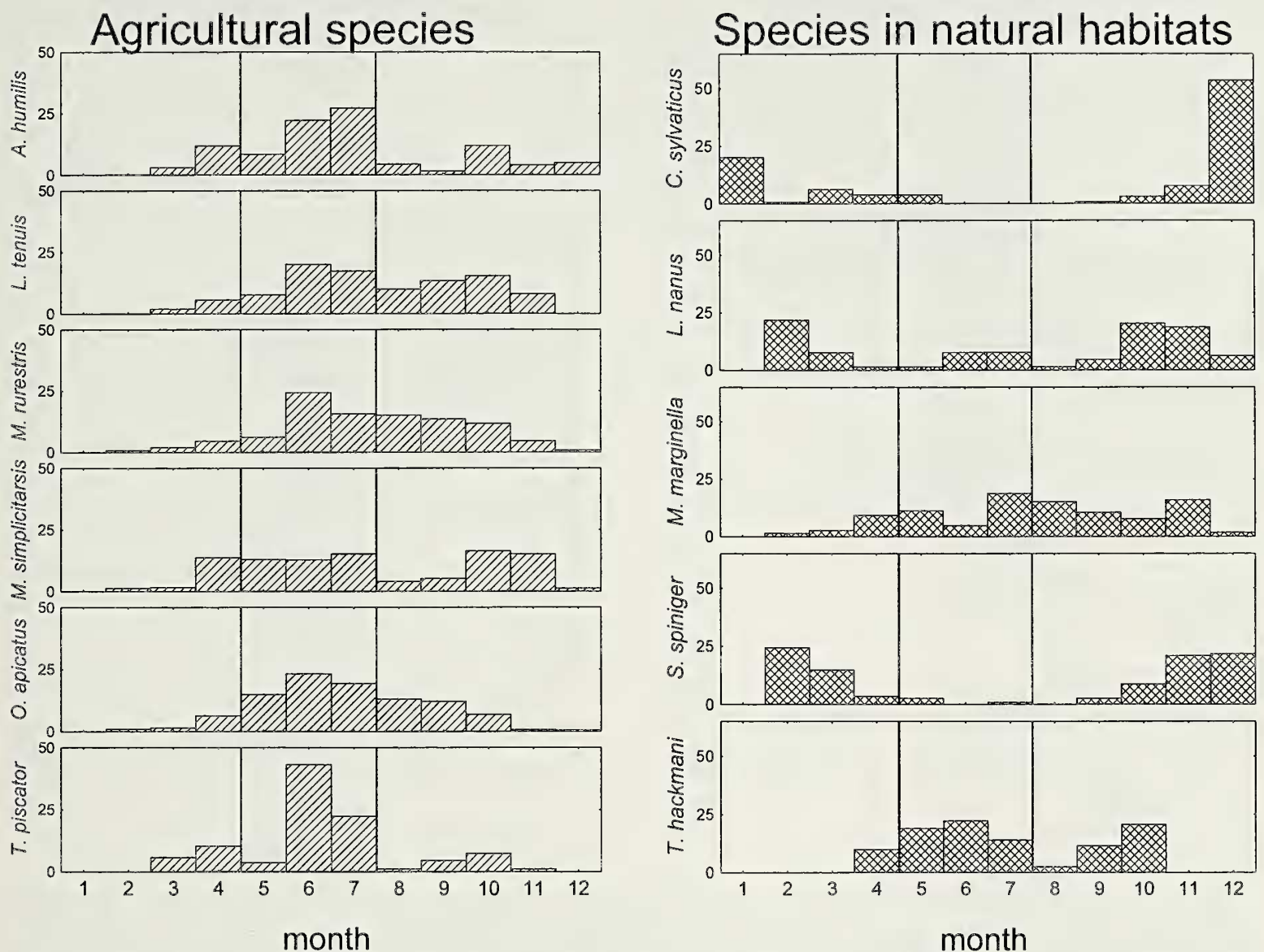


Figure 6.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Linyphiidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Centromerus sylvaticus*, *Leptyphantus nanus*, *Minicia marginella*, *Sintula spiniger*, *Trichoncus hackmani*.

rated from the random field (Fig. 3). The Soerensen similarity, also known as Bray-Curtis or Czekanowski similarity, is a proportion coefficient in city-block space. As compared to Euclidean distance it retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune & Mefford 1999).

Considering the first 10 dominant species in cereal fields, the distance between fields in terms of species composition (1-Soerensen similarity) showed no significant relationship to the geographical distance for either sampling methods (Mantel test, suction sampling: $n = 4$, $R = 0.19$, ns, pitfall: $n = 6$, $R = 0.35$, ns, McCune & Mefford 1999), thus no regional effect on agrobiont composition can be inferred.

The uniformity of agrobiont composition seems to be a generality that is valid for a

limited geographical area, such as Hungary. In this study only “arable agrobionts” are considered, but the identity of “agrobionts” is also strongly crop dependent. Different agrobionts can be found in structurally or otherwise radically different systems, such as orchards (Jenser et al. 1999) or rice (unpublished data), but within a range of only broadly similar crops, such as in alfalfa and cereals in the present study, no difference in the agrobiont composition could be shown. The agrobiont nature of individual species also shows geographical variation. Comparing the present data set with data of agrobionts in other European studies (Hänggi et al. 1995), for Central-Europe, four core arable agrobionts could be identified: *Meioneta rurestris* (C.L. Koch 1836), *Pachygnatha degeeri* Sundevall 1830, *Oedothorax apicatus* (Blackwall

Theridiidae life cycles

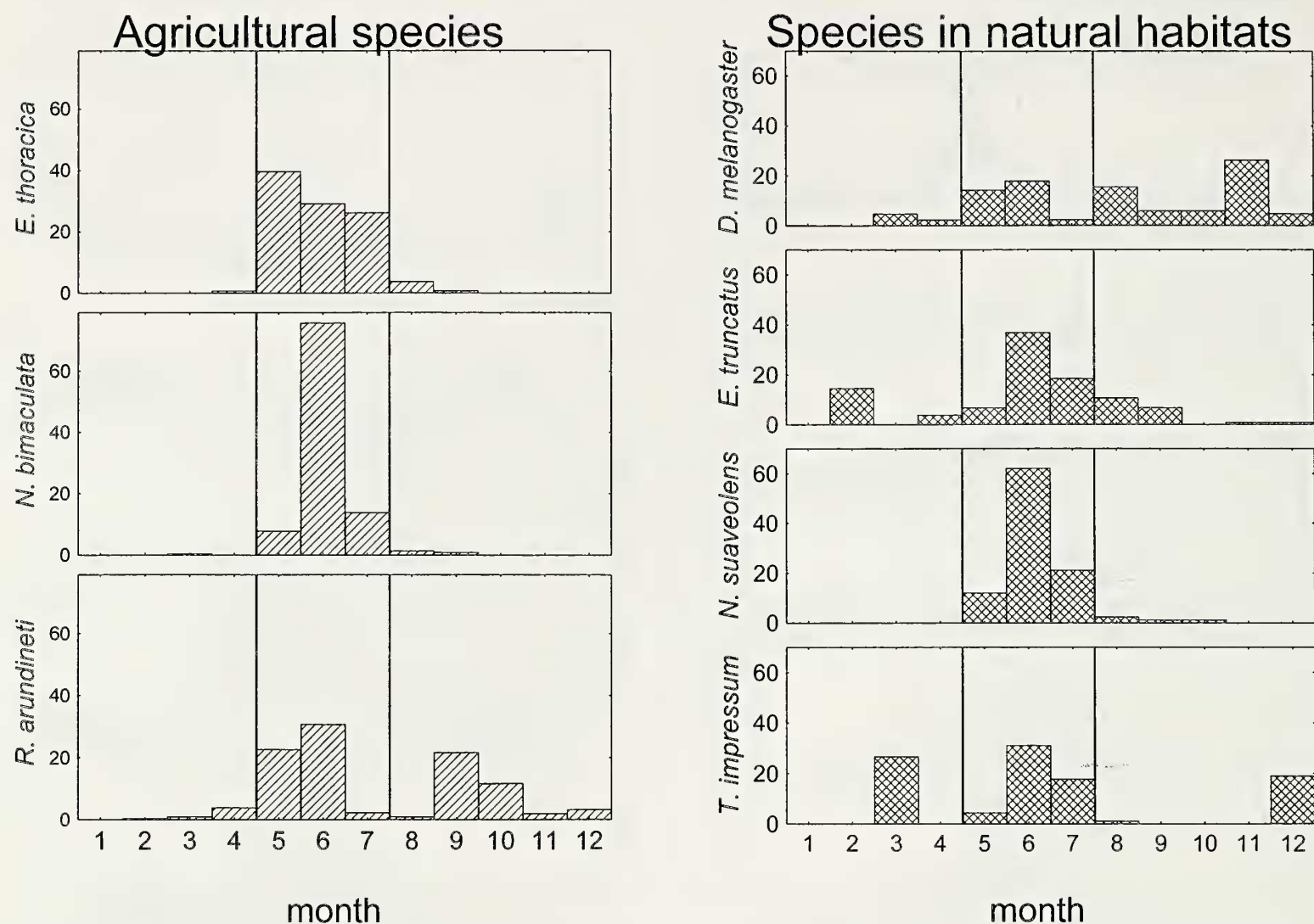


Figure 7.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Theridiidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Enoplognatha thoracica*, *Neottiura bimaculata*, *N. suaveolens*, *Diplocephalus melanogaster*, *Episopus truncatus*, *Theridion impressum*.

1850) and *Erigone dentipalpis* (Wider 1834). Other species, like the most abundant in Hungary, *Pardosa agrestis* (Westring 1861), show a strong North-West South-East geographical gradient in their association with agricultural systems (Blick et al. 2000). One of the major agrobionts of North-West Europe, *Lepthyphantes tenuis* (Blackwall 1852) shows an opposite gradient, and can be listed only as an agrophile in Hungary. *Pardosa agrestis* has a shift in life cycle along the same gradient; it has one generation per year in Northern Europe (S. Toft pers. comm.), and has two generations in Hungary (Samu et al. 1998). This parallel change in life cycle and agrobiont tendency suggests again the importance of life history characteristics for being successful in agricultural systems.

Habitat preference of agrobionts.—In Hungary agrobionts (first eight species of Table 2) were virtually only dominant in arable

fields. In secondary grassland habitat patches they represented a modest portion (13.6%) of the total spider fauna, and their overall presence was minimal (6%) in all studied natural grassland habitat types (Fig. 4). The indicator species analysis showed, that agrobiont species are not widespread generalists, that would occur in a wide range of habitat types. If agrobionts were wide-tolerance, eurytopic generalists, then they should not be indicators of either of the considered main habitat types. This hypothesis was falsified by finding that in all arable-grassland comparisons nearly all agrobionts showed up as indicators of the agricultural habitat (Table 3). On the other hand, indicator species analysis, by not providing any agrobiont as an indicator in the alfalfa-cereal comparison, reinforced the finding of the field-by-field comparison, that the same dominant species occurred in all arable fields, irrespective of crop type.

Gnaphosidae life cycles

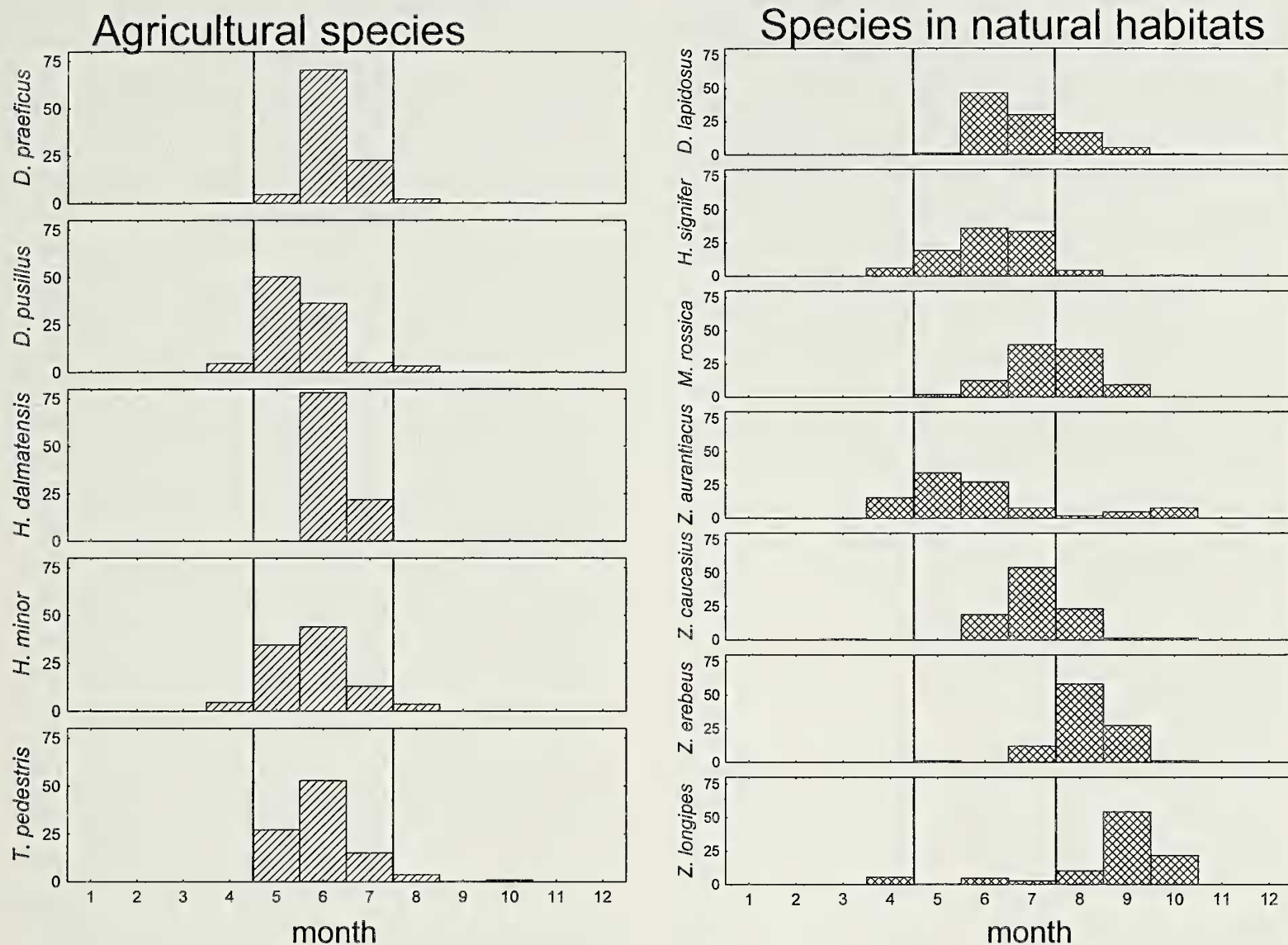


Figure 8.—Life cycle of natural habitat vs. agrobiont and agrophile species belonging to the Gnaphosidae. The histograms indicate the occurrence of adult individuals as percentage of all adults caught from the given species. Species as in Table 2. Those not listed there: *Drassyllus praeficus*, *D. pusillus*, *Drassodes lapidosus*, *Haplodrassus dalmatensis*, *H. minor*, *H. signifer*, *Micaria rossica*, *Trachyzelotes pedestris*, *Zelotes aurantiacus*, *Z. caucasicus*, *Z. erebeus*, *Z. longipes*.

The scope of the present study was not wide enough to indicate the full range of natural habitats agrobionts occupy. We have extracted the habitat preferences of nine agrobiont species from Hänggi et al.'s (1995) database of Central European spiders (Table 4). These data are from the literature, and encompass a wide range of different habitats. The survey shows that, taking this broader view, agricultural habitats are still the most preferred ones for agrobionts. We think that both the Hungarian data (Fig. 4) and the data in Table 4 show that it cannot be stated as a general rule, that agrobionts are originally hygrophilous species that are native in littoral areas (Raatikainen & Huhta 1968; Luczak 1979). In our view, the essence is not the hygric nature of the native habitat; the disturbance pattern is more important. From the Eu-

ropean survey it emerges that agrobionts are abundant in abiotically driven, frequently disturbed and/or pioneer areas, but they are less frequent in mesic, stable habitat types.

The APEH hypothesis (Wissinger 1997) concerns the adaptedness of agrobiont invertebrates, and makes a specific prediction about the disturbance pattern in their native habitat, namely that they originate from predictably ephemeral habitats. *Pardosa agrestis* in Hungary seems to provide a nice case for APEH, because its main natural habitats are saline marshes (Szita et al. 1998) that are annually flooded during the spring and autumn rainfall maximums, and are dry in between. Both disturbance periods coincide with the presence of small-medium sized juveniles, the possible colonizer stage (Richter 1970), while the species is known to reproduce in June (and also

in August), during the relatively stable period in its habitats. This again draws our attention to the importance of life cycle synchronization with habitat and landscape dynamics.

Life cycle of agrobionts.—To study life history adaptation of agrobionts to arable systems, we chose more species than the first 10 most dominant ones. We selected species from the four most prevalent families present in Hungarian arable systems (Lycosidae, Linyphiidae, Gnaphosidae and Theridiidae) by the criteria that they showed a clear preference for either arable or natural habitat types, and we possessed enough data to plot adult phenology (Figs. 5–8). Phenology curves showed that species occurring in natural habitats, in all four families, had a more varied phenology. Although agricultural species showed variation, they considerably synchronized their first generation with the main vegetation period of arable crops (which in Hungary is May–July). The onset of the favorable size of the crop (May) seemed to be the strongest factor that limited the energy, and therefore prey demanding maturation and reproduction for most agricultural species. None of the 18 species we examined had an adult peak before May, while 6 of the 22 species from natural habitats had an early spring adult peak. Some agricultural species could make use of the post harvest period by producing a second generation (e.g., *Pardosa agrestis* and *Robertus arundineti*). Some Linyphiidae species are known to have multiple generations per year (Topping & Sunderland 1998). Here the main peak also coincided with the May–July period, but adults seemed to be present somewhat earlier, as well as later on in the year.

Synchronization with habitat changes was also noted by Toft (1989). During the main crop growing period, May–July, environmental conditions are fairly stable, the maturing crop provides sufficient prey and shelter from abiotic disturbances. Such a life cycle pattern supports the APEH hypothesis. Agrobionts make use of the predictably occurring good period by maturing and reproducing during that time. Arable habitats are likely to be colonized by younger instars (by most families, except for Linyphiidae) and dispersed from in late summer and autumn. A literature survey shows (Sunderland & Samu 2000) that field margins and hedgerows provide fewer colonizers, and population movements are likely

to be between fields of different crops and/or management stages.

CONCLUSIONS

Based on ten years of survey data on Hungarian arable field spider communities, we can generalize both about the structure of agricultural spider communities and about the ecological nature of their most dominant species, the agrobionts. We found that the skewed dominance structure of agricultural communities is invariable both in our data sets and in the literature. The skew is caused by the over-dominance of a few agrobionts; typically less than 10 species make up 60–90% of the whole spider community. The remaining part of agricultural communities was rather variable, causing large differences in species richness values in individual fields. Nevertheless, a high diversity of spiders in arable fields was detected, which might have implications in conservation.

The agrobiont segment of arable spider communities showed very little field-by-field variation, and within Hungary no regional effects could be detected. Agrobiont species were always the most dominant in agricultural habitats, and occurred only sporadically in natural habitats, thus they can be regarded as specialists of the agricultural habitat type. For larger geographical regions, even if the potential species pool were the same, climate related life history variations might cause different species to become successful agrobionts in certain regions, and to be absent from agricultural communities in others. Agrobionts, by and large, came from frequently disturbed, pioneer, or otherwise abiotically driven habitats, but the usually not very clear (and regionally also potentially variable) habitat preference of agrobionts makes it difficult to test specific theories, like APEH, except for certain well studied species. The life cycle of agrobionts and agrophile species nearly unequivocally showed synchronization with the main crop growth period, which provides indirect support for the APEH hypothesis.

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